Bureau of Mineral Resources, Geology & Geophysics

RECORD

RECORD 1989/17

IOC Workshop report:
BENTHIC MICROBES & REEFS

Townsville, Australia, August 1988

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1. AIMS OF THE WORKSHOP

The Workshop was organised as a contribution to both the programmes of the Intergovernmental Oceanographic Commission and the International Geological Correlation Programme 261 STROMATOLITES. It was convened during the Sixth International Coral Reef Symposium, 8th-12th August in Townsville. Invitation to participate was extended to all participants in IGCP Project 261, to all members of the Coral Reef section of the InternationalAssociation of Biological Oceanographers and to other interested scientists. The emphasis was on discussion with contributors delivering short 10 minute formal presentations. Topics to be covered by the Workshop included:-

- * Benthic sediment micro-organisms in present day reef systems
- * Primary production by microalgae & cyanobacteria in reefs
- * Microbial calcification
- * Bacterial production
- * Benthic microbes and their rôles in forming reefs through geological history

The programme for the workshop consisted of an introduction, state of the art reviews scientific contributions and their discussion, and development of future programmes and projects.

1. ADMINISTRATIVE ARRANGEMENTS

1.1. Designation of the Chairman and Rapporteur

The positions of Chairman and Rapporteur were shared by the co-convenors of the workshop; Dr Robert V Burne (Bureau of Mineral Resources,Canberra City ACT 2601,Australia) and Dr Judith A Hansen (School of Biological Sciences A12, University of Sydney, Sydney NSW 2006, Australia).

2. OPENING OF THE WORKSHOP

Dr Robert Burne and Dr Judith Hansen welcomed the participants at the Geology Department, James Cook University of North Queensland on 8th August 1988. They passed on the good wishes for the success of the workshop that had been sent by Dr Peter Davies, Chairman of the Coral Reef Committee of the International Organisation of Biological Oceanographers, Dr Endre Dudich, IGCP Secretary, and Dr Mario Ruivo, IOC Secretary.

3. STATE OF THE ART REVIEWS

REEFS DOMINATED BY BENTHIC MICROBIAL COMMUNITIES; THEIR HISTORY AND PRESENT LIMITATIONS

Robert V Burne

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The purpose of this workshop is to examine the changing role that Benthic Microbial Communities have played in the formation of ecological reefs from their first appearence in the Proterozoic to the present day. The topic is of particular interest to many reef scientists. Reefs are carbonate build-ups that form either from the skeletal remains of sedentary organisms or from their activities in binding sediment of promoting calcification. An ecological reef is an organically bound wave resistant topographical structure. It is an entity of its own making and forms a sedimentary system within itself. Most present-day reefs are composed of hermatypic scleractinians, coralline algae, and other organisms together forming an association with biological and ecological diversity probably greater than any comparable association in earlier geological history. This is related to a very high order of trophic integration and organisation which is perhaps more complex than that of any other major ecosystem. However analogous structures were constructed before the evolution of higher life forms prior to .5 Ga B P by Benthic Microbial Communities (BMCs). BMCs can be complex associations of photosynthetic prokaryotes, eukaryotic microalgae and chemoautotrophic and chemoheterotrophic microbes, They have evolved from prokaryotic ancestors that, as a result of their interaction with sediment to form organosedimentary structures, formed the first macroscopic record of life on Earth. Indeed, for the first 3 Ga of the 3.5 Ga history of life on this planet, the only macroscopic evidence of life lay in the organosedimentary structures formed in association with the gradually evolving BMCs. These structures, which include the well-known stromatolites, have been termed microbialites, and frequently developed large reefs in shallow seas that represent the early analogues of today's coral reefs.

The gradual rise of higher life-forms over the past .5 Ga has been accompanied by a decline in the relative importance of benthic microbial sedimentation, despite an increasing tendency for it to produce calcified structures, with their place being taken by a succesion of skeletal metazoans capable of secreting robust skeletons culminating in the evolution of the scleractinian corals in the Tertiary. Today it dominates only in specialised environments which include hot springs, some lakes and hypersaline marine embayments. This decline through time is poorly understood, but is probably due either to increasing grazing pressure or competition. The growth rates of modern subtidal calcareous microbialites are an order of magnitude less than the growth rates of coral reefs at comparable latitudes. Nevertheless it is certain that microbial sedimentation is playing a very significant though poorly documented part in the construction of reef framework at the present time. Present day coral reefs are similar to other shallow marine habitats in that sunlight is the driving force and there are interactions between the benthic and water column systems. However Coral Reefs differ significantly from other shallow-water systems in that a considerable proportion of the primary producers are animals with photosynthetic symbionts e.g. hard and soft corals and to a lesser extent tridacnid clams and sponges. Thus the benthic microbial community still plays an important though rather indirect role in the construction of the reef framework. However, although today benthic microbes are active in the degradation of organic material within the reef and in the cycling of nutrients, the main primary production is undertaken by zooaxanthellae symbiotic with the corals, and by coralline and other macro-algae. BMCs form turfs in the deeper parts of the fore-reef, and some cavity fillings are well laminated and are interpreted by some as stromatolites thought this view has been challenged. It is perhaps significant that a large proportion of the non-symbiotic primary production in present-day reefs is consumed directly by grazing organisms.

Present-day coral reefs occur in clear ocean or shelf waters which generally contain low concentrations of inorganic nutrients and sparse plankton populations. It is essential, therefore, that coral reefs have efficient methods to fix and retain essential nutrient elements. Reef systems are dependant on microbes for nitrogen derived from N_2 fixation and the photosynthesis of organic compounds which sustain nutritional and energy requirements for non-photosynthetic organanisms in the communities. Benthic microbial communities are very efficient in providing biochemical cycling within the community that can sustain it even though the overlying waters are depleted in essential nutrients. Coral reefs contain a mix of different habitats which are generally consistent in different geographical regions. These habitats include the coral dominated fore-reef slope, the turbulent crest zone, the algal dominated reef flat, the sand covered lagoon and usually some form of back-reef structure descending into deeper water for platform or atoll reefs. Similar environments can be identified in ancient reefs, and even in Early Proterozoic times carbonate platforms had developed which show the full range of facies once thought to be typical only of the Phanerozoic, and throughout the Proterozoic BMCs constructed reefs of many types, including Barrier, Pinnacle & Patch Reefs. Compared to these ancient reefs, A modern coral reef has a particularly high diversity of organisms, hence there are many trophic networks operating at different levels and on differing scales. The current knowledge of microorganisms in these systems is sparse, being obtained only from a limited number of short term studies. Anaerobic processes are particularly poorly understood and have been largely ignored because much of the sediment is physically disturbed or radically bioturbated and therefore not particularly anoxic.

It is hoped that this workshop will provide new insights into the role of benthic microbial communities in modern reefs, and through this an increased understandingof their importance in building reefs in the geological past.

MICROBIAL ECOLOGY OF PRESENT-DAY BENTHIC CORAL REEF COMMUNITIES

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In this paper recent studies of bacterial processes on coral reefs are reviewed.
Bacterial biomass and production rates have been measured in sediments of a number of reefs on the Great Barrier Reef. Production rates generally range from 130 - 740 $\mathrm{mgC} . \mathrm{m}^{-2} . \mathrm{d}^{-1}$ integrated over the top 1 cm of sediment with marked seasonal and spatial variations. In sand flat and lagoon sediments, bacterial production rates are higher in summer than in winter. Bacterial production rates in surface sediments are equivalent to those on the carbonate surfaces of patch reefs and reef flat pavement. However, bacterial production is greater in the sediments when integrated over the whole sediment column, since bacterial growth rates are rapid to about 10 cm depth.
Coral reef sediments receive large amounts of particulate organic matter exported as detritus from the reef front and reef flat. Little is known of the biochemical composition of the detritus which includes coral mucus, fecal material and fragments of reef flat turf algae.

There is little information on the importance of bacteria as a food source for benthic macrofauna in coral reefs. Detritus such as algal fragments and mucus may be consumed directly by macrofauna. There are no studies concerning the relative importance of detritus, bacterial, microalgal carbon as food sources for consumers. Benthic macrofauna are known to influence the distribution and activity of microorganisms. Thalassinid shrimps, holothurians and gastropods can all affect either biomass and production of bacteria or microalgae.

Anaerobic processes may be important in decomposition of organic matter on coral reefs. Even coarse reef flat sediments which appear to be highly oxidized ore often anoxic below 0.5-1cm depth. Although sulfate reduction rates are generally lower in reef sediments than in other coastal ecosystems, they can account for up to 20% of benthic community respiration, with highest rates in the top few centimeters of sediment. Methane production is usually low or undetectable in surface sediments on coral reefs, however the presence of methane in reef carbonate framework indicates that aneraboic diagenesis may be important in that environment.

Nitrogen cycling on reefs has been the subject of several reviews and will not be treated in detail here. Although nitrogen fixation has been invoked as a major source of nitrogen to support reef primary production, at One Tree reef in the Great Barrier reef, nitrogen supplied through nitrogen fixation has been shown to account for an amount equivalent to about 10% of that required to support observed rates of primary production. This indicates that remineralization by heterotrophic microorganisms may be much more important in supplying nitrogen for primary production. In addition denitrification rates on reefs may be significant, thus representing a loss of nitrogen to the coral reef ecosystem.

Many recent studies have focussed on the distribution and activity of benthic microorganisms on reefs, but little is known of the fate of bacterial production or the factors controlling microbial abundance and metabolism. Further studies are needed to elucidate the role of bacteria as food for consumers and the significance of factors such as supply of organic matter or predation in regulating bacterial activity.

4. CASE STUDIES

4.1. Community Budgets

"COULD CHEMIOSMOSIS WORK AT THE COMMUNITY LEVEL?" -

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Peter Mitchell's chemiosmotic hypothesis explains how energy is conserved in ATP via a charge separation across biological membranes. Among other things, the hypothesis applies to both pro- and eucaryotes, and describes how respiration can be uncoupled from both electron transport as well as ATP synthesis. Thus, ATP production efficiency is related to proton-motive forces (analogous to EMF) established by charge separation, and not directly to the electronc transport system or to substrate-level phosphorylation per se. Perhaps this phenomenon could work at the community level (especially in sedimentary systems that have redox gradients) and help explain why systems such as coral reefs are so productive.

It is proposed that gradients of both pe and pH that are produced and maintained by excretions of sedimentary microbes (augmented by spontaneous chemical reactions in this regime) can increase the efficiency of ATP production (therefore anabolism) within the gradients. Life in such a "battery" may be a vestige of evolution (sensu Rich, 1984) that persists in presently oxidized habitats. In this sense, we can no longer explain community budgets or flow of mass and energy as direct causal relationships between eucaryotic production and heterotroiphic catabolism.

4.2. Anaerobic Processes

NET SULFATE REDUCTION AND METHANOGENESIS RATES WITHIN THE UPPER METER OF A REEF FRAMEWORK

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Oxidation of organic matter within the upper meter of the framework of Checker Reef (Kaneohe Bay, Oahu) results in the depletion of dissolved oxygen and a build-up of sulfide and methane. Average sulfide concentrations in the top one meter of the reef framework were 10-380 µM; average methane concentrations were 14-387 nM. A rain-induced dilution of the surface waters of the bay was used as a natural tracer to measure mixing rates between surface water and the upper meter of the Checker Reef framework.

Interstitial water residence times for the upper meter of the framework ranged from 2.6-5.9 days, with an average of 3.8 days. These residence times, combined with measured sulfide and methane pool sizes, permit calculation of net in situ production rates within the upper meter of the reef framework. These values range from 1.6-146.5 µM sulfide/d, with an average of 38.2 µM sulfide/d; and 2.4-148.8 nM methane/d, with an average of 48.9 nM/d. These are minimum estimates of production because the formation of iron sulfides and methane oxidation are also known to occur within the framework.

MICROBIALLY-MEDIATED ANAEROBIC DIAGENESIS WITHIN CORAL REEFS AND OTHER MARINE CARBONATE FRAMEWORKS

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We have analyzed the interstitial waters of a variety of lithified marine carbonate frameworks of Recent, Pleistocene, and Eocene age, and have found their chemical compositions to be quite similar. In all cases the oxygen concentrations were very low, and there were elevated levels of the end-products of microbial organic matter oxidation (e.g., sulfide, methane, dissolved inorganic carbon, ammonia, and phosphate). We conclude that anaerobic diagenesis is a common feature of such systems, and may have an important role in their geochemistry at both microscopic and macroscopic scales.

4.3. Miocrobial Destruction of Reefs

BORING ALGAE : THE DILIGENT DESTROYERS

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Boring algae date from the Precambrian, and hence have potentially been able to attack any shell ever formed in the photic zone. Their boring traces are common in shells of all ages; in fact, changes in intensity of algal borings have been used to infer that growth rates of Ordovician rugose corals were similar to those of modern reef corals. On modern reefs, boring algae may be found in every coral head and every carbonate sediment grain in the photic zone. Notwithstanding the demonstrated importance of this group, little work has been done on them. The approach of most coral reef workers has been to ignore the existence of boring algae. We need to know much more of the activities of this group, especially their effect on reef sediment budgets and reef metabolic studies. For example, recent experimental evidence suggests that the "half-life" of a carbonate sand in a shallow tropical lagoon may be only a few decades, due to dissolution by algae, and other observations indicate that much of the flux of dissolved gases around corals is controlled by the activities of boring algae.

THE ROLE OF BACTERIA IN SEDIMENTATION DAMAGE TO REEF CORALS

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Sediment deposition on reef corals occurs naturally or may be accelerated due to man-made disturbances such as dredging. The cause of sedimentation damage to corals has been ascribed to lack of light, food and oxygen. Field and aquarium experiments were carried out in the Philippines and Hawaii to investigate the process of tissue damage to corals following sediment deposition. Fifty scleractinian species were subjected to sediment deposition ranging from 20 to 40 mg/cm2/day. In all cases where tissue necrosis led to death of a portion of a colony, sediment overlying those areas became discolored and gave off a sulfurous odor. The antibiotic tetracycline was used to test for the involvement of bacterial in the process of tissue necrosis due to sedimentation. Colonies of *Oxypora glabra*, an Indo-Pacific reef coral with a low tolerance to sedimentation were held in aquaria filled with tetracycline treated water (1, 10 and 100 mg/l)and subjected to sedimentation. The speed and extent of tissue necrosis was assessed. Colonies held in aquaria without tetracycline treated water showed initial tissue necrosis after 1 day; 50% were dead after 5 days and all were dead after 7 days. When tetracycline was added to the seawater, tissue necrosis due to sediment deposition began after 2 days, but necrosis did not affect more than 15% of the colony surface and none of the colonies died. Similar experiments conducted with 2 Hawaiian species (*Montipora verrucosa* and *Pocillopora meandrina*) showed a signficant decrease ($p<0.05$) in percent of the colony surface damaged by sedimentation when tetracycline was added to the seawater. The results indicate that bacteria are involved in the process of tissue necrosis and may be partially responsible for coral mortality following sediment deposition.

4.4. Planktic Microbes and Reefs

TRICHODESMIUM RED TIDES IN THE GREAT BARRIER REEF LAGOON-SCIENTIFIC CURIOSITY OR ENVIRONMENTAL THREAT TO THE REEF

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Studies at Townsville in the central section of the Great Barrier Reef Lagoon (GBRL) have shown that blooms of the cyanobacteria Trichodesmium mobilises trace and toxic metal ions such as casmium, lead, copper and nickel in coastal waters where this algae accumulates. This enrichment of toxic metal ions is entirely a natural process, and seems to be associated with the production of high concentrations of marine humic acis from Trichodesmium filaments and the production of highly fluorescing 'iron-rich' particles that are up to 5% rich in iron. It is believed that this fact has considerable environmental signficance in those regions of Australia where this algae accumulates, particularly enclosed embayments, and in regions of Australia where this algae has accumulated in the past. Blooms of this algae can on occasions extend for many hundreds of kilometres along the Queensland coast, extending from the shoreline to the outer barrier reef, and occupying tens of thousands of square kilometres of sea surface. This unique blue-green algae is prolific off the west coast of Australia, in the Dampier Archipelago, and occurs at different times of the year from Rottnest Island off Perth to the Northwest Shelf. It comes as no surprise therefore that blooms of Trichodesmium have been captured by Space Shuttle photography and retrospective Landsat imagery.

In conclusion it is believed that this phenomenon is one of the most significant enviornmental processes in the GBRL. Studies are necessary to answer such questions as are the blooms a necessary part of the GBRL's ecology? What has been the intensity of bloom formation in the past? Is the phenomenon being influenced by human activities, or is this natural process being affected by climatic changes? Is the phenomenon more characteristics of the central GBRL or is it specific to the whole lagoon, and if so is this mobilisation of toxic ions affecting the ecology of the corals.

BUGS IN THE BEACH SAND

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That microbes are in some way implicated in the genesis and diagenesis of reefs and associated environments has been known for some time but as with most geological studies their incisive study has been left to the cognate disciplines for our own lack of ability to cope with the complex biochemical calculations required for genetic analysis. Thus a substantial literature on this theme has developed over the last decade which is little known to traditional geologists. For this reason, following many years of frustrating petrographic observations on fossil materials, a reconnaissance study of a stranding algal bloom was undertaken with a view to establishing some basic standards to facilitate discussion with colleagues in the cognate disciplines which are better able to undertake some of the experiments that we as geologists need to be run in order to keep our evolutionary hypotheses in perspective. The stranding materials from cool temperate storms and tropical blooms yield contrasting features. The latter would appear to stand a good chance of preservation and complement preliminary observations on fabrics generated in open circulating seawater aquaria.

4.5. Microbial Calcification

MECHANISMS OF CALCIFICATION IN ALGAE & BACTERIA: TERMINOLOGY & THEORY

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CaCo3 formation in algae and bacteria can be broadly classified into three mechanisms, biologically induced, biologically mediated, and biologically controlled calcification. In biologically induced calcification the organism simply acts as a site for CaCO3 nucleation and the deposits are of 'normal' crystallography and largely unordered. In biologically mediated calcification the organism not only takes part in nucleation, but may also affect crystallography and crystal organisation. In biologically controlled calcification , the organism exerts strong control over both nucleation and crystal growth. In the latter calcification is usually intracellular. Examples of biologically induced calcification are Halimeda, Chara (but not the oogonia) and some cyanophytes. Biologically mediated calcification occurs in the coralline red algae and a number of sheath -calcifying cyanophytes.The main example of biologically controlled calcification is the formation of coccoliths by chrysophyte algae.

CLASSIFICATION OF MICROBIAL CARBONATES

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The history of the development of ideas concerning stromatolites is instructive in understanding these and other microbial deposits. But it is also true that the intricacies of the uncertainties and confusions along this path readily obscure the results of this research during the past century. The fact is that we can now recognize a variety of benthic calcareous deposits formed primarily by microbial organisms such as bacteria, cyanobacteria and algae.

The processes of formation of microbial carbonates are : 1. trapping of sedimentary particles; 2. calcification (biomineralization) of organic tissues; 3. surficial precipitation of minerals on organisms and/or associated sediment. There are four principal products of these processes : stromatolites, dendrolites, thrombolites, travertine.

Sediment trapping is the main process involved in the formation of agglutinated stromatolites. Inorganic surface mineralization is dominant in tufa stromatolites. Biomineralization is responsible for the formation of skeletal stromatolites, dendrolites (term introduced here for biomineralized microbial deposits with a dominant dendritic macrofabric), and thrombolites. Both biomineralization and inorganic mineralization are involved in the formation of microbial travertine.

4.6.Present-Day Microbial Build-ups.

PRESENT-DAY MICROBIAL REEFS OF LAKE CLIFTON & SHARK BAY, WESTERN AUSTRALIA

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The gradual evolution of higher life forms since the end of the Proterozoic introduced pressures of competition and predation that displaced benthic microbial communities (BMCs) from the position of being the major reef-builders of the world's oceans. However, BMCs have continued to form the ecological basis for carbonate reef development in various specialised environments. throughout the Phanerozoic. Two present-day examples of microbialite reefs occur in Western Australia. Hamelin Pool is a hypersaline marine embayment of Shark Bay in which corals and many molluscs are excluded and stromatolitic microbialites flourish. Lake Clifton is a hyposaline coastal interdunal lake in which thrombolitic microbialites exist as part of a specialised non-marine ecosystem.

In both areas microbialites grow in shallow waters and have coalesced near the shores to form extensive rigid carbonate platforms. The top of the platform is emergent , but the front is an active growth face which passes offshore into an area of isolated microbialites interspersed with unconsolidated sediments. There is a marked zonation with variations in microbialite morphology apparently being determined mostly by environmental factors. The internal structures of microbialites seem to be determined more by biological factors.

The fact that intertidal mats constructed by BMCs are limited to extreme environments free of gasteropod grazing pressure has led some workers to the view that microbialites can only develop today in what are otherwise biological deserts. This is far from the truth, as the reefs of both Hamelin Pool and Lake Clifton forming the basis of diverse eco-systems in which the BMCs act as food sources, while the rigid microbialites that they produce provide both shelter for animals and a firm substrate for sessile plants. While it is difficult to obtain precise data, growth rates determined for both the reef systems indicate that their rate of vertical growth is an order of magnitude less than that of their coral counterparts.

Studies of these areas have emphasised that the microbialites have similarities with their Proterozoic ancestors and regard them as living fossils.However this obscures the fact that they are contemporary eco-systems that are relatively highly evolved when compared with their Proterozoic counterparts, e.g. the importance of diatoms.
Benthic microbial communities include the primary producers of the microbial reef systems and they are also integral to the process of frame building. In both areas the most significant accretion takes place in submerged environments. In Lake Clifton the submerged BMC includes diatoms and the cyanobacteria Scytonema . The calcified structure results from crystal nucleation on the microbial sheath, and not within the cell walls. At Hamelin Pool the submerged BMC includes the coccoid cyanobacteri Entophysalis as well as diatoms. Here a significant proportion of the calcified structure is the result of carbonate sediment detritus adhering to or being trapped and bound by the microbial community. This material has a finer size range than that of the surrounding sediment. The detrtus is then cemented by the prcipitation of carbonate soon after deposition. It this stage it is not clear to what extent this process of cementation is microbially controlled. Other BMCs occur within both systems. Thus BMCs dominated by Microcoleus, and Lyngbia occur at various levels within the intertidal zone in Hamelin Pool, with distributions determined partly by degrees of inundation, but showing significant interpenetration at zone boundaries. The BMCs typically have a vertical zonation and include components that degrade organic matter and play an important part in concentrating and recycling nutrients within the living benthic layer. The nature of the BMC has a strong influence on the process of lithification, and hence on the internal structure of the microbialites.

The combination of active primary production and the constructionof a rigid wave-resistant structure form the basis of ecosystems that, while not rivalling those of coral reefs in diversity or biomass, are nevertheless considerably more productive and diverse than those which exist in the waters of Lake Clifton or Hamelin Pool where microbial reefs have not developed.Exhaustive biological surveys have yet to be undertaken in these reef systems. In Lake Clifton amphipods and Isopods occur in the fenestrae below the surface of the microbiolites. Numerous gastropod, ostracod and bivalve shells are also found incorporated into the microbialite structure. In view of the grazing habits of the crustaceans it is reasonable to assume that the microbialites provide a source of food as well as refuge from predation. The shrimps congregate around the reef by day , apparently seeking protection from the sun and from prdation by numerous birds. Two species of small fish also concentrate amongst the microbialites, some sheltering beneath overhangs and in cavities. Trichopteran Larval cases are found attached in sheltered places beneath and within some microbialites. Polychaetes are found associated with the structures. Bryozoan remains are incorporated in some microbialites. The Charophyte Lamprothamnium papulosum , a green alga which favours oligotrophic waters and which grows throughout the lake, also attaches to the microbialites. Recently the macroalgae Cladophora has been found in increasding numbers attached to the microbialite. The colonisation of this algae may be related to an increase in the nutrient loading of the lake waters related to human settlement of the lakes eastern shore over the past decade. A species of Sea Anenonie is found on the microbialites and colonising intervening sediment.

In Hamelin Pool the BMCs are associated with a meiofauna of nematodes. Cavities in the lithified microbialites are occupied by fish and crustaceans, some in symbiotic relationships, as well as by bivalves. Coralline algae and sponges colonise the firm substrate, especially favouring sheltered and overhanging sites, and foraminifera, annelids, and gastropods also contribute to the benthic community. Sessile plants such as the calcifying alga Acetabularia and Brown algae attach to the firm substrates provided by the lithified structures, which provide shelter for fifteen species of fish, as well as sea snakes.

The morphological variation of the reefs however appear to be controlled more by extrinsic factors. As with coral reefs , microbial reef development favours windward locations. It has been suggested that this provides a means of winnowing fine sediment from the system that might otherwise drown the reef. BMCs have a greater capacity to survive sediment burial than do corals, but because of slow rates of lithification (c.f. that of corals) the require a relatively sediment free environment to accrete a calcified structure. Water-level exerts a control on the upper margin of microbial calcification, with most growth appearing to take place in the permanently submerged zone, and growth diminishing rapidly with frequency of inundation. There is evidence of a fall in datum level in both areas within the past 1-2000 years. This complicates the interpretation of the morphological zonation.

Near the north eastern margin of Lake Clifton a reef flat has developed. It is composed of the coalesced remains of microbialites displaying concentric structues that represent either domical forms that have been planed off, or represent growth structures equivalent to the micro-atolls of the coral reef flat. The higher parts of the flat are colonised by cyanobacterial mats, sustained in part by ground water resurgence that forms a slight moat at the landwards margin of the flat. The front of the reef flat is relatively sharp with the platform of coalesced domes giving way to isolated submerged domes interspersed with unconsolidated sediment. Off shore the domes pass into conical structures, often with an apical crater. these pass lakeward into unconsolidated lake sediment. The factor limiting the lakeward margin of reef growth is not clear, though it may be related to the availability of resurging alkaline groundwaters. Elsewhere in the lake mirobialites rise as isolated pinnacles 1.6m high. these have flat tops, apparently determined by low lake level.

Reef flats also exist in Hamelin Pool in locations of exposure to waves. Subtidal stromtolites stranded by Recent sea-level fall have coalesced and have been infilled by sediment to form a reef flat often coated by a hard crust. these areas are laterally interposed with areas of cyanobacterial mat colonisation. The crest of the reef is marked by a rim of botryoidal masses of radial aragonite, possibly marking the rapid calcification of entophysalis dominated BMC. The face of the reef is an overhanging visor of active growth. Offshore the stromatolites form mounds. they icrease in size in deeper water and in places show a tendency tio grow columnar forms on the tops of the mound. elsewhere the deeper water forms are low bulbous ridges orientated normal to the shore. Again the lower limit of colonisastion is relatively sharp, and is not well understood.

The morphological variety and zonation of the reefs appears to be extrinsically controlled. The growth rates of the microbial structures can be estmated bay radio carbon dating and indicate a growth rate of .3-1 mm a year- an order of magnitude less than that of coral reef framework.

STROMATOLITES FROM AN AREA OF SHARK BAY, WESTERN AUSTRALIA, CHARACTERISED BY NEAR NORMAL MARINE SALINITIES

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It is widely accepted that stromatolites are found almost exclusively in specialised environments which include hot springs, some lakes, and hypersaline marine embayments. The absence of grazing pressure in these environments is invoked to explain why stromatolites can exist there but are rare in normal marine settings, and why stromatolites appear to have been much more common during the Precambrian than during the Phanerozoic.

This paper reports on a new stromatolite locality in Herald Bight, Shark Bay, Western Australia, where modern stromatolites can be found in waters characterised by near normal marine salinities; the waters range in salinity from about 37ppt in winter to about 42ppt in suimmer. These stromatolites form a band about 15m wide and 100m long in the intertidal zone, and extend from isolated clumps of mangroves in the south to calcareous sandy beach deposits in the north. Shoreward of the stromatolites, sandy beach deposits are separated from salt/clay pans 'birridas' by low coastal dunes; seawards, the sediment is dominated by calcareous sands which are covered by extensive seagrass meadows below the low tide ldevel. Herald Bight contains some of best fishing grounds in Shark Bay, and is notable both for the abundance and diversity of marine fauna.

The existence of stromatolites in Herald Bight indicates that they can develop in areas of near normal marine salinity where there is a high grazing potential. Hence there must be some additional, as yet undetermined, factor which influences trhe distribution of modern stromatolites. Near the stromatolites in Herald Bight, low salinity (<8ppt.) ground water seeps out to the surface for several months following heavy rains, at high tide goats can sometimes be observed standing in the sea drinking the upwelling fresh water. It may be that this periodic fresh water seepage aids the development of the stromatolites by causing changes in salinity which exclude potentially competitive organisms.

MODERN CALCAREOUS MICROBIALITES ASSOCIATED WITH CORAL REEFS

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Modern calcareous microbialites called "kopara" presently accrete in shallow lakes located on the top of French Polynesian atolls rims. The lake waters are mixtures of dominant non-marine (water table + rain inputs) and marine waters (sea/lagoon, due to infiltrations through coastal bars and invasions during cyclones). Their chemistry consequently fluctuates between those of marine and fresh waters : they are generally brackish, never hpersaline. (1) the lakes are quasi-exclusively colonised by benthic microbial communities dominated by Monera, (2) the composition of the atolls substrates (only carbonates, essentially Ca) induces the mineralization of kopara under a purety carbonated form. Its mineral fraction is composed of in situ - precipitated high-magnesian calcite, sometimes accompanied by small quantities of detrital coralline aragonite (deposited in the lakes by sea/lagoon invasions). The high-magnesian calcite is precipitated under biological influence, as can be deduced from its close spatial relations with the cyanobacterial sheaths and the three-dimentional organic network constituting the "backbone" of kopara. This network is generated by the reorganization of polysaccharidic microfibres issued from the decomposition of decaying Cyanobacteria. The resulting bulk structure of kopara is stromatolitic, the carbonates being concentrated within millemetric to centimetric thick, more or less horizontal laminae, alternating with pur organic ones. The intermediate environmental situation of kopara between marine and freshwater settings is probably responsible for its particular features among other modern calcareous microbialites.

Indeed, modern stromatolites essentially accrete in marine environents and get mineralized by trapping and binding of detrital particles, whereas biologically influenced calcificiation is claimed to occur only in freshwater environments 1n between these two types, kopara is a stromatolitic sediment mineralized under biological influence.

4.7. Ancient Microbial Build-ups

CARBONATES OF POSSIBLE MICROBIAL ORIGIN ON SOUTHWESTERN MARGIN OF CHILKA LAKE (RAMBHA REGION, ORISSA), EAST COAST OF INDIA

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Loosely distributed carbonate nodules and relatively more continuous, irregularly protruberating, sheet-like, dense carbonates of 2-3m approx. thickness occur closely associated with loose to slightly consolidated argillaceous siliciclastics having some quartz sand and very fine to fine gravels underneath an alluvial-clayey overburden of about 3m in excavations in areas of Rambha, Diadei, Madhurchua (approx. area 3 x 1.5 Km) and Binchanapalli, Radhagovindpur, Sipakuda (approx. area 1.5 x 0.75 Km) on the southwestern margin of lagoonal Chilka Lake connecting to the Bay of Bengal on east coast of India. The deposits occur between the high-water line of Chilka Lake and foot-hills of the coastal hill ranges of the Precambrian Eastern Ghats belt. Generally, the isolated nodules measure from a centimetre to about 5 cm or even more and are distributed within argillaceous siliciclastics. Surface textures of the carbonates may be knobby, papillose or rugose. Thin section texture shows fabrics having dense cloudy micritic patches, microspares of different size gradations, patches of blocky pore-filling calcite, empty pores, spongy patches, vague filamentous structures, irregular laminations, dark clots, probable reworked peloidal clast with yellowish coatings. Textural inhomogeneity locally has given rise to a bizzare fabric. Quartz grains and argillaceous impurities are associated. It is suggested that the nodules and sheets formed microbial lithostromes on the lake margin due to activity of benthic microbial community in shallow peripheral lacustrine waters during the late Holocene. The marginal water body of the Chilka Lake has receded subsequently.

STROMATOLITE; OF HIRAPUR PHOSPHORITE FORMATION OF BIJAWAR GROUP OF ROCKS, CENTRAL INDIA

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Stromatolites have been recorded, associated with the Hirapur-Phosphate Formation of Bijawar Group of rocks of Proterozoic epoch. This is for the first time that such association of the stromatolite have been reported in the Bijawar phosphogenic system. Stromatolite are dwarf, (few inches to a foot long column) and characterised by the laminated-flat-domical - to collonella, kusseilla and oncolitic forms species. Earlier in the absence of stromatolite; in the Hirapur phosphorite deposit it was described as non-biogenic origin, but the present discovery of the stromatolite indicated that the phosphorite deposit of the Bijawar proterozoic-phosphogenic-system has been attributed by the biogenic processes. Sedimentary structure-ripple marks, rhythmic-lamination, current bedding and stromatolites indicated that the deposition of the phosphorite has occurred at shallow-marginal, photic zone around-subtidal to supratidal zone.

STROMATOLITIC CRUSTS IN THE FRAMEWORK OF WENLOCKIAN REEFS OF ENGLAND

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Coral and bryozoan skeletons of the framework of the patch reefs in the Much Wenlock Limestone Formation of the Silurian of the Welsh Borderland U.K. commonly are draped in a banded micrite crust, similar in structure to stromatolites. These crusts are not found in off-reef beds and the microenvironment of anastomosing reef framework is thought essential for their development. The crusts appear to have sedimented into position yet behaved rigidly during reef growth suggesting marine cementation.

5. DISCUSSION

Participants at the workshop were enthusiastic about the value of such a multidisciplinary exercise which brought together scientists with experience of microbial ecology, coral reef research, sedimentology, biogeochemistry, and geology.

Discussion initially focussed on what we can learn from studies on present-day sediment-microbial communities that can help towards an understanding of past formation of stromatolites? Two points seemed to be significant: grazing pressure and competition. The observation of I G Hunter (University of Alberta) that stromatolites developed inplace of coral reefs in the Cayman Islands when environments became restricted during the Quaternary supports the suggestion that competition by scleractinians and coralline algae may be significant in limiting the development of marine stromatolites at the present day.

The poor level of understanding of microbial processes in modern reefs is in part due to the high level of small scale variability - why does this occur? We need research utilising small microprobes to isolate the causes of this variability. We do need to know the nature of small scaleprocesses, e.g. what % of total carbon goes through these microbes? In all published accounts of reef microbial ecology it is necessary to define the scale to be examined, and it is important to define the questions that are being asked so as to be able to define the scale at which must work. Most studies have looked at micro-environments within 1 coral for example - these data cannot be extrapolated to the whole reef because of enormous variability within the reef system. More information is needed on what scale this variability is occuring at. Compare this to studies of plankton communities where they ignore much of the spatial variability to get at the "Big Picture". Concentration of bacteria varies on a scale of only 10cm or less and this must be overcome by increasing sample sizes. When looking at primary productivity need to define the scales being examined, and this is equally true of the effects of the anaerobic activity within the sediments: a lot of microniches are present in any one reef environment, together representing many different habitats in which very different processes are occuring. How can we model the whole system with our current poor understanding?

Much work has shown that in reef systems there is often an effect of deposit-feeders and burrowers on micro-algae, but not on the bacteria. However, in temperate systems the activity of polychaetes and other burrowing animals can have an effect on microbial communities. There is a need to gather further data on the factors controlling rates of grazing of microbial communities in various environments, and those factors that protect the communities from grazing. One factor is calcification. This is poorly understood. Relatively few cyanobacteria are involved in calcification. Respirationleads to dissolution of $CaCO_3$ at night. Heterotrophic bacterial activity needs to be considered in developing a model of an anaerobic closed system. Here, with saturation state increasing, there will be a big influence of sulphate reduction with sulphide scavenged by aragonite.Ideas about anaerobic activity - energy cycling - carbonate precipitation and dissolution need to be pursued.

Cyanobacteria also differ in their ability to overcome sedimentation. Filimentous oscillatorians move at 10 µm/sec in loose sediment and can therefore keep pace with sediment burial, while coccoid cyanobacteria have limited motility and must recolonise the sediment surface after burial.

Heavily calcified cyanobacteria were not present in the Proterozoic, instead thses forms seemed tohave depended more on the trapping and binding of sediment. The classification of microbial carbonates recognises many genetically distinct types, including: Agglutinates, Travertine, Thrombolites, Tufa, Dendrolites, Iso-ooids, Ooids and Microbial Oncolites. These types of microbial carbonate need to be linked to environmental and biological controls, and their differing distribution through geological time explained.

People working on modern microbial sedimentation need to develop closer comparisons with ancient examples.

6. RECOMMENDATIONS

6.1. The Workshop recommended that attention be focussed on the microbial contribution to the functioning of coral reef ecosystems with repect to materials budgets, nutrient fluxes, biogeochemistry and trphic interactions. Attention should be paid to integrating the data obtained from various environments and microniches into a model representative of the reef as a whole.

6.2. The Workshop recognised the need to examine the role of microbes in the destruction and erosion of reefs, and the ability of microbial communities to colonise dead reef tracts.

6.3. The Workshop recommended that consideration be given to the environmental, physicochemical, and biological controls on microbial calcification, and the likely rates at which this processes may proceed be documented.

6.4. The Workshop concluded that studies of modern microbial ecosystems could usefully adopt similar interdisciplinary research strategies to those applied to modern coral reefs, and that results drawn from these studies should be used to examine possible analogies with ancient microbial systems fom the Proterozoic and the Phanerozoic.

6.5. The Workshop endorsed the recommendadtion of the 5th International Symposium on Fossil Cnidaria that countries should compile an inventory of its known occurrences of reefs and organic buildups, following the initiativeof the Canadian Reef

Inventory Project. Particulary attention should be given to the understanding of the contribution of benthic microbes to the formation of such reefs.

7. ADOPTION OF REPORT

The Workshop adopted the Summary Report and the Rcommendations therein.

8. CLOSURE OF THE WORKSHOP

The convenors thanked the participants for their contributions to a successful meeting. They also thanked the organizing committee of the 6th Coral Reef Symposium, and support staff of James Cook University for their assistance in organising the meeting.
The Workshop was closed at 11.30 pm on August 1988.

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